Detection of quantitative trait loci for growth and carcass composition in cattle[1,2]

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ABSTRACT: The objective of the present study was to detect quantitative trait loci for economically important traits in a family from a *Bos indicus* × *Bos taurus* sire. A Brahman × Hereford sire was used to develop a half-sib family (n = 547). The sire was mated to *Bos taurus* cows. Traits analyzed were birth (kg) and weaning weights (kg); hot carcass weight (kg); marbling score; longissimus area (cm^2); USDA yield grade; estimated kidney, pelvic, and heart fat (%); fat thickness (cm); fat yield (%); and retail product yield (%). Meat tenderness was measured as Warner-Bratzler shear force (kg) at 3 and 14 d postmortem. Two hundred and thirty-eight markers were genotyped in 185 offspring. One hundred and thirty markers were used to genotype the remaining 362 offspring. A total of 312 markers were used in the final analysis. Seventy-four markers were common to both groups. Significant QTL (expected number of false-positives < 0.05) were observed for birth weight and longissimus area on chromosome 5, for longissimus area on chromosome 6, for retail product yield on chromosome 9, for birth weight on chromosome 21, and for marbling score on chromosome 23. Evidence suggesting (expected number of false-positives < 1) the presence of QTL was detected for several traits. Putative QTL for birth weight were detected on chromosomes 1, 2, and 3, and for weaning weight on chromosome 29. For hot carcass weight, QTL were detected on chromosomes 10, 18, and 29. Four QTL for yield grade were identified on chromosomes 2, 11, 14, and 19. Three QTL for fat thickness were detected on chromosomes 2, 3, 7, and 14. For marbling score, QTL were identified on chromosomes 3, 10, 14, and 27. Four QTL were identified for retail product yield on chromosomes 12, 18, 19, and 29. A QTL for estimated kidney, pelvic, and heart fat was detected on chromosome 15, and a QTL for meat tenderness measured as Warner-Bratzler shear force at 3 d postmortem was identified on chromosome 20. Two QTL were detected for meat tenderness measured as Warner-Bratzler shear force at 14 d postmortem on chromosomes 20 and 29. These results present a complete scan in all available progeny in this family. Regions underlying QTL need to be assessed in other populations.

Key Words: Beef, Carcass Traits, Genetic Markers, Quantitative Trait Loci

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Introduction

Genetic markers and linkage maps have provided tools to detect QTL for economically important traits in cattle (Stone et al., 1999; Casas et al., 2000; Casas et al., 2001; MacNeil and Grosz, 2002). Quantitative trait loci will potentially improve genetic progress, especially for traits difficult or expensive to measure, through marker-assisted selection. Carcass composition and meat quality traits are among those that would benefit most from the use of genetic marker information.

An initial effort to identify QTL by selective genotyping 187 offspring from this family has been reported by Stone et al. (1999). They selected 94 individuals with extreme performance for retail product yield and fat thickness, and the remaining 93 individuals were selected for extremes in meat tenderness measured as Warner-Bratzler shear force (Keele et al., 1999; Stone et al., 1999). Evidence supported the presence of loci influencing carcass composition and meat quality traits on chromosomes 1, 2, 5, and 13. The objective of the present study was to detect QTL using the entire family from a *Bos indicus* × *Bos taurus* sire. This report presents the completed scan in all available progeny.

[1]Mention of a trade name, proprietary product, or specified equipment does not constitute a guarantee or warranty by the USDA and does not imply approval to the exclusion of other products that may be suitable.

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Materials and Methods

Animals

A half-sib family was developed using a Brahman × Hereford sire. The bull was previously used in the USDA reference population to generate the cattle linkage map (Kappes et al., 1997). The sire was mated to Hereford, Angus, and F_1 cows from the Germplasm Evaluation Project Cycle IV to produce 288 offspring in 1994. The sire was mated to MARC III (¼ Hereford, ¼ Angus, ¼ Red Poll, and ¼ Pinzgauer) cows to produce 259 offspring in 1996 (547 animals total). Breeds of sires for the F_1 cows were Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nellore, Piedmontese, or Salers. Breeds of dams for the F_1 cows were Hereford or Angus. Calves were weaned at an average of 187 d and raised from weaning to slaughter on a corn-corn silage diet. Cattle were serially slaughtered at a commercial packing plant and the wholesale rib was obtained from the right side of each carcass for dissection (Shackelford et al., 1995) and for determination of longissimus Warner-Bratzler shear force. Average age at slaughter was 455 d.

Traits Analyzed

Offspring were evaluated for growth, carcass composition, and meat quality traits. Birth (kg) and weaning weights (kg) were recorded. Carcass traits evaluated were hot carcass weight (kg); fat thickness (cm); marbling score; longissimus area (cm^2); USDA yield grade; and estimated kidney, pelvic, and heart fat (%). Carcass traits predicted from the rib dissection were retail product yield (%) and fat yield (%). Meat tenderness was measured as Warner-Bratzler shear force (kg) at 3 and 14 d postmortem. To measure Warner-Bratzler shear force, steaks were thawed, cooked, and sheared as described by Wheeler et al. (1998). Means, standard errors, and standard deviations for traits are in Table 1.

Genomic Screen

Development of the bovine genetic map at the U.S. Meat Animal Research Center (Kappes et al., 1997; http://www.marc.usda.gov) has resulted in availability of genetic markers throughout the genome. Primary screening of this family was conducted using 238 microsatellite markers in 185 offspring (Stone et al., 1999). In the current study, 130 markers were used to genotype the remaining 362 offspring. Of these markers, 74 were common to both groups. A total of 312 markers were used in the final analysis covering 2,850 centimorgans. Informative markers in the sire were chosen based on their location in each chromosome and ease of scoring. Amplification reactions for each marker were done with purified DNA extracted from blood with a saturated salt procedure (Miller et al., 1988). Amplification conditions have been described elsewhere (Kappes et al., 1997).

Table 1. Mean, standard errors, and standard deviations (SD) for birth weight (BWT); weaning weight (WWT); hot carcass weight (HCW); marbling (MAR); longissimus area (LMA); USDA yield grade (YG); estimated kidney, heart, and pelvic fat (KPH); fat depth (FAT); fat yield (FATYD); retail product yield (RPYD); and meat tenderness measured as Warner-Bratzler shear force at d 3 (WBS3) and 14 (WBS14) postmortem

Trait	Mean ± SE	SD
BWT, kg	43.1 ± 0.2	5.33
WWT, kg	214.7 ± 1.0	54.1
HCW, kg	330.2 ± 1.2	27.9
MAR[a]	522 ± 2	56.4
LMA, cm^2	76.5 ± 0.3	7.0
YG	3.15 ± 0.03	0.64
KPH, %	3.09 ± 0.02	0.52
FAT, cm	1.10 ± 0.02	0.42
FATYD, %	25.2 ± 0.2	4.0
RPYD, %	61.9 ± 0.1	3.2
WBS3, kg	5.34 ± 0.05	1.25
WBS14, kg	4.09 ± 0.04	0.88

[a]NAR: 400 = slight^{00}, 500 = small^{00}.

Statistical Analysis

An *F*-statistic profile was generated at 1-cM intervals for each chromosome by regression of phenotype on the conditional probability of receiving the Brahman allele. Data were analyzed using the approach suggested by Haley et al. (1994), with a model that included effects of sex (heifers or steers), year of birth (1994 or 1996), dam line within year of birth, and days on feed as a covariate. The conditional probabilities of inheriting the Brahman allele were calculated with a FORTRAN program. Analysis for each chromosome was generated using the procedure GLM from SAS (SAS Inst., Inc., Cary, NC). The LOD drop-off method was used to calculate support interval for each putative QTL (Ott, 1992).

The experimentwise threshold value was calculated according to Lander and Kruglyak (1995). An *F*-statistic was considered suggestive of linkage if it exceeded a value of $F = 10.0$ (one expected false-positive per genomic scan; **ENFP** = 1), and significant if it exceeded a threshold of $F = 16.7$ (one false-positive per 20 genomic scans; ENFP = 0.05). These results correspond to a nominal *P*-value of $P = 0.002$ and $P = 0.00005$, respectively.

Results

Regions identified as harboring significant QTL for growth, carcass composition, and meat quality traits reside on chromosomes 5, 6, 9, 21, and 23 (Figures 1 to 5). Chromosomes with evidence suggesting the presence of putative QTL are summarized in Table 2.

Table 2. Relative position, support interval, and allelic effects of putative QTL detected with a suggestive threshold

Chromosome and trait	Relative position, cM[c]	Support interval, cM[c]	Effect (B-H)[d]	F[e]	P_n[f]	P_g[g]
1						
BWT[a]	120	100–135	2.59 kg	10.9	0.001	0.67
2						
YG[a]	52	38–79	–0.22	11.8	0.0006	0.70
FAT[a]	54	21–60	–0.142 cm	11.5	0.0007	0.50
BWT[a]	59	31–75	1.86 kg	13.5	0.0003	0.21
3						
MAR[ab]	28	0–42	–20.14	12.2	0.0005	0.38
FAT[a]	36	23–46	–0.13 cm	10.7	0.001	0.73
BWT[a]	40	21–58	1.89 kg	13.0	0.003	0.26
7						
FAT[a]	55	44–71	–0.18 cm	15.0	0.0001	0.10
10						
MAR[ab]	4	0–28	25.5	11.0	0.0009	0.64
HCW[a]	24	0–30	–9.7	12.0	0.0006	0.41
11						
YG[a]	66	27–80	–0.22	11.9	0.0006	0.43
12						
RPYD[a]	60	43–64	1.36%	14.1	0.0002	0.16
14						
FAT[a]	16	0–22	–0.15 cm	13.2	0.0003	0.24
YG[a]	19	0–24	–0.23	13.0	0.0003	0.26
MAR[ab]	47	30–87	19.9	11.8	0.0006	0.45
15						
KPH[a]	45	21–69	–0.23%	11.1	0.0009	0.60
18						
HCW[a]	23	11–38	–8.9 kg	10.6	0.001	0.76
RPYD[a]	85	79–85	1.1%	11.9	0.0006	0.43
19						
RPYD[a]	5	0–15	–1.49%	13.4	0.0002	0.22
YG[a]	18	0–37	0.26	12.2	0.0005	0.37
20						
WBS3[a]	66	55–75	–0.44 kg	13.6	0.0002	0.20
WBS14[a]	72	52–75	–0.29 kg	11.0	0.0009	0.64
27						
MAR[a,b]	29	12–51	21.2	11.6	0.0007	0.48
29						
RPYD[a]	49	40–62	–1.03%	12.4	0.0005	0.34
HCW[a]	54	45–58	9.5 kg	14.4	0.0002	0.14
WBS14[a]	54	30–65	0.25 kg	10.1	0.002	0.95
WWT[a]	55	42–57	7.8 kg	13.4	0.0002	0.22

[a]BWT = birth weight; WWT = weaning weight; HCW = hot carcass weight; MAR = marbling; LMA = longissimus area; YG = USDA yield grade; KPH = estimated kidney; heart and pelvic fat; FAT = fat depth; FATYD = fat yield; RPYD = retail product yield; WBS3 = meat tenderness measured as Warner-Bratzler shear force at d 3 postmortem; and WBS14 = meat tenderness measured as Warner-Bratzler shear force at d 14 postmortem.

[b]MAR: 400 = slight[00], 500 = small[00].

[c]cM = relative position in centimorgans from the beginning of the linkage group according to Kappes et al. (1997).

[d]B = Brahman; H = Hereford.

[e]Maximum *F*-statistic in the interval.

[f]Probability of false-positive for a single test.

[g]Expected number of false positive per scan (Lander and Kruglyak, 1995).

A chromosomal region with effects on birth weight, marbling, longissimus area, and fat yield was identified on chromosome 5 (Figure 1). The maximum *F*-statistics for the traits in this chromosome were detected between centimorgans 53 and 75 from the beginning of the linkage group. Birth weight and longissimus were significant (ENFP = 0.0007 and 0.05, respectively), whereas evidence supporting the presence of QTL for marbling score (ENFP = 0.2) and fat yield (ENFP = 0.73) was suggestive. The support intervals for birth weight, longissimus area, marbling score, and fat yield spanned centimorgans 42 to 68, 38 to 66, 62 to 80, and 53 to 71, respectively. Animals inheriting the Brahman allele were 2.64 kg heavier at birth than animals inheriting the Hereford allele. Animals inheriting the Hereford allele had a greater longissimus area (2.85 cm^2), a

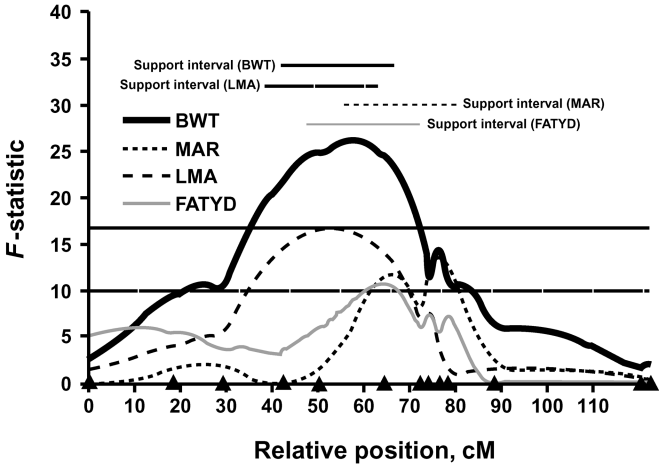

Figure 1. *F*-statistic profile and support interval for birth weight (BWT), marbling (MAR), longissimus area (LMA), and fat yield (FATYD) on bovine chromosome 5. The upper horizontal line represents the significant threshold ($F = 16.7$), and the lower horizontal line represents the suggestive threshold ($F = 10.0$). Triangles on the x-axis indicate the relative position of markers BMS1095, BP1, RM103, BMC1009, BL37, BR2936, CSSM022, IGF-1, BMS1216, RM029, BMS1248, BMS597, and BM8126.

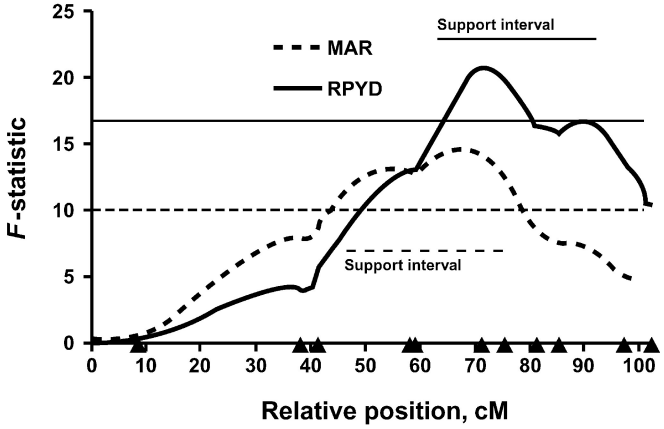

Figure 3. *F*-statistic profile and support interval for marbling (MAR) and retail product yield (RPYD) on bovine chromosome 9. The upper horizontal line represents the significant threshold ($F = 16.7$), and the lower horizontal line represents the suggestive threshold ($F = 10.0$). Triangles on the x-axis indicate the relative position of markers MB009, BMS817, CSSM025, BMS1290, BY24, TGLA73, BM7209, BMS2251, BM4208, BMS1943, and BMS1967.

higher marbling score (20.4 units), and greater fat yield (1.2%) when compared with animals inheriting the Brahman allele.

A significant (ENFP = 0.03) QTL for longissimus area was detected on chromosome 6 (Figure 2). The maximum *F*-statistic was located at centimorgan 9, in the centromeric region of the chromosome. The support interval ranged from centimorgans 0 to 26 from the beginning of the linkage map. Offspring inheriting the Hereford allele had a 2.8-cm^2 greater longissimus area when compared to offspring inheriting the Brahman allele.

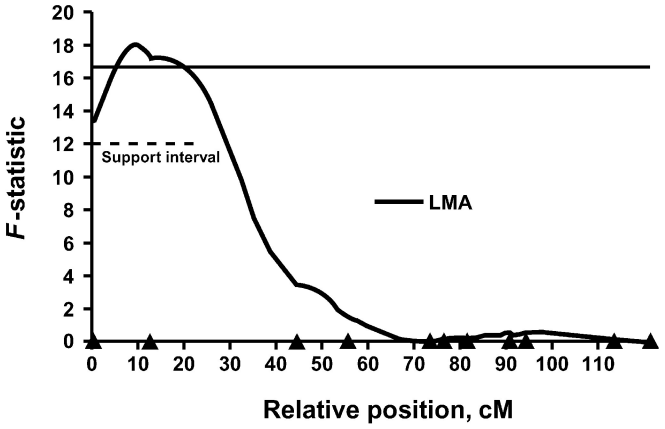

Figure 2. *F*-statistic profile and support interval for longissimus area (LMA) on bovine chromosome 6. The horizontal line represents the significant threshold ($F = 16.7$). Triangles on the x-axis indicate the relative position of markers ILSTS093, ILSTS090, BMS2508, BMS518, BM4621, BM415, EL03, ILSTS018, BP7, BM8124, BMC4203, and BL1038.

There was evidence supporting the presence of QTL significant for retail product yield (ENFP = 0.008) and suggestive for marbling score (ENFP = 0.13) on chromosome 9 (Figure 3). The maximum *F*-statistic for both traits was between centimorgans 67 and 71. Figure 3 also shows the support intervals that were calculated for retail product yield (from centimorgans 63 to 92) and for marbling score (from centimorgans 46 to 76). Animals inheriting the Hereford allele from the sire had 1.46% less retail product yield and 21.7 units more of marbling score when compared with animals inheriting the Brahman allele.

Figure 4 shows the *F*-statistic profile for a significant QTL (ENFP = 3×10^{-8}) for birth weight in the centromeric region of chromosome 21. The support interval for this trait encompassed centimorgans 0 to 10 with the maximum *F*-statistic on centimorgan 3. Those inheriting the Brahman allele were 3.47 kg heavier at birth, compared to those that inherited the Hereford allele.

Chromosome 23 harbors a significant (ENFP = 0.009) QTL for marbling score (Figure 5). The maximum *F*-statistic for this QTL is at centimorgan 32, and the support interval goes from centimorgans 21 to 42. In this case, animals inheriting the Brahman allele from the sire had a higher marbling score (26.1 units) when compared to animals inheriting the Hereford allele.

Chromosomal regions with suggestive support for presence of putative QTL are summarized on Table 2. Evidence of putative QTL existed on 14 chromosomes.

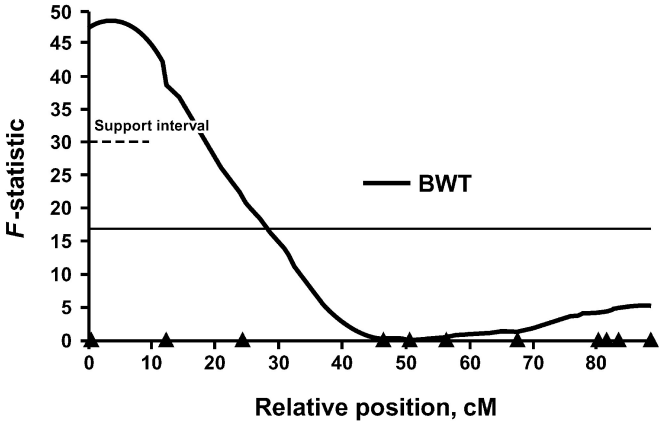

Figure 4. *F*-statistic profile and support interval for birth weight (BWT) on bovine chromosome 21. The horizontal line represents the significant threshold ($F = 16.7$). Triangles on the x-axis indicate the relative position of markers BM8115, RM151, ILSTS095, BMS2815, ILSTS016, TGLA337, TGLA122, BMS670, IDVGA-30, OY3, and BMS2382.

Chromosomes 2, 3, 10, 14, 18, 19, 20, and 29 may harbor QTL for more than one trait.

Discussion

Two QTL for meat tenderness were detected. One of these is on chromosome 20, affecting Warner-Bratzler shear force at 3 and 14 d postmortem, and the other is on chromosome 29 for Warner-Bratzler shear force at 14 d postmortem. The latter was detected in the same chromosomal region as a previously reported QTL for this trait in a resource population obtained from a crossbred sire from Piedmontese and Angus (Casas et al., 2000). Smith et al. (2000) identified CAPN1 as a candidate gene in this region of chromosome 29, and Page et al. (2002) have identified single nucleotide polymorphisms that produce amino acid changes that are associated with differences in tenderness. Quantitative trait loci detected in this study indicate the presence of a gene, or group of genes, influencing meat tenderness in the telomeric region of bovine chromosome 29.

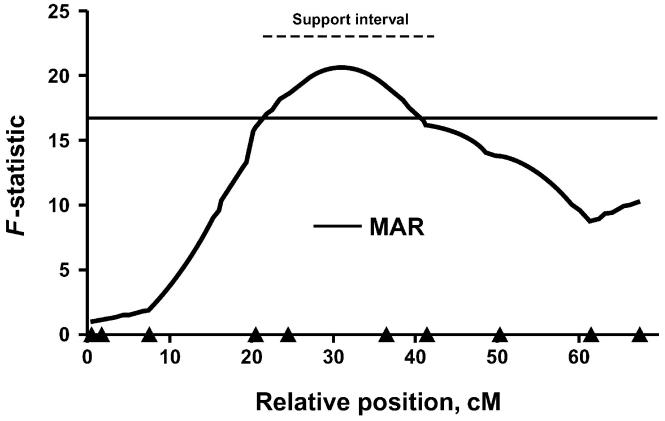

Figure 5. *F*-statistic profile and support interval for marbling (MAR) on bovine chromosome 23. The horizontal line represents the significance threshold ($F = 16.7$). Triangles on the x-axis indicate the relative position of markers INRA064, INRA132, CSSM005, VEGF, BM1258, BMS468, BY11, BM7233, BMS2269, and BM1443.

Chromosome 29 has been identified as harboring QTL for weaning weight, retail product yield, hot carcass weight, and Warner-Bratzler shear force measured at 14 d postmortem. Support intervals indicate that all QTL lie between centimorgans 30 and 65. In previous studies (Casas et al., 2000; Page et al., 2002), only QTL for Warner-Bratzler shear force had been detected.

A QTL on chromosome 20 affecting meat tenderness at 3 and 14 d postmortem was detected. This is the first report of this QTL. It will be important to identify candidate genes for this QTL, to ascertain their association with these traits in other populations.

Warner-Bratzler shear force is an objective measure of meat tenderness. Inconsistency of meat tenderness is a major issue facing the beef industry. Increased *Bos indicus* inheritance has been associated with increased meat toughness (Crouse et al., 1989). If validated, QTL for meat tenderness can be used to select for *Bos indicus* sires that produce meat with low shear force value. Keele et al. (1999), using offspring born in 1994 from the family used in the present study, identified a QTL on bovine chromosome 15 that affected meat tenderness measured as Warner-Bratzler shear force at 14 d postmortem in one of four slaughter groups. It is plausible the QTL detected in the one slaughter group is really a false-positive. Alternatively, it is likely that unknown environmental factors played a key role in masking this QTL in the remaining groups. It is uncertain whether this QTL could be validated in outbred populations because these factors were unidentified.

Marbling score is an estimation of the level of intramuscular fat deposition at the 12- to 13th-rib region of the longissimus. Several QTL were detected for marbling score. A QTL for marbling was detected between centimorgans 46 and 76 for marbling score on chromosome 9. Georges et al. (1995) detected a significant QTL for fat yield in this chromosome in dairy cattle. Data presented by Georges et al. (1995) indicates that both QTL, the one for marbling score and the one for milk fat yield, reside in a similar location. It could be hypothesized that the same gene or genes in this genomic region could be responsible for production of fat that is deposited intramuscularly, and deposited in milk in beef and dairy cattle, respectively.

Evidence exists for a QTL affecting marbling score on chromosome 3. The most likely location of the QTL is between centimorgans 0 and 42. Casas et al. (2001) detected a QTL for marbling score in a family obtained from a crossbred Belgian Blue and MARC III sire on chromosome 3, spanning from centimorgans 40 to 90. It is unlikely that the same gene, or group of genes,

underlying this trait on chromosome 3 are influencing the same trait in this chromosome. Differences in breed composition may influence the expression of different genes affecting marbling score.

Two candidate genes have been identified for the QTL for marbling score on chromosome 5. Barendse (1999) indicates that alleles at the retinoic acid receptor-gamma and at the retinol dehyrogenase genes have been associated with differences in marbling score. The former gene is associated with the molecular marker CSSM034, located at 45.1 centimorgans from the beginning of the linkage group of chromosome 5 (Kappes et al., 1997), whereas the latter gene is associated with the marker ETH210, located at 70.0 centimorgans. Comparing the location of these genes with the quantitative trait locus for marbling score on chromosome 5 (Figure 1), it is observed that only the retinol dehydrogenase gene could be considered candidate to explain its variation. Markers at or near this gene would need to be evaluated in this population to ascertain its effect on marbling score.

There is evidence suggesting that a QTL for marbling score exists in the centromeric region of chromosome 10. The support interval for a QTL affecting marbling score on chromosome 10 spans centimorgans 0 to 28. Casas et al. (2001) detected a QTL for marbling score in the same chromosome, but it resided around centimorgan 60. This indicates that at least two QTL could be segregating for the same trait in this chromosome.

Casas et al. (2000) detected a QTL for marbling score on the telomeric region of chromosome 27. A QTL for the same trait was detected on chromosome 27 in the present study; however, the location of the QTL in both studies is different. The support interval for the most likely position of the QTL for marbling score is between centimorgans 12 and 51. Again, evidence exists for more than one QTL affecting marbling score on the same chromosome in different studies.

Quantitative trait loci for fat thickness; fat yield; and estimated kidney, pelvic, and heart fat were detected in several chromosomes. Two of these QTL could be similar to those detected for fat production in other studies. Casas et al. (2000) presented evidence of a QTL for fat thickness between centimorgans 50 and 80 from the beginning of the linkage group of chromosome 5. The most likely position of the QTL for fat yield on chromosome 5 is between centimorgans 53 and 71. This information indicates that both QTL are located in a similar region of chromosome 5. This supports the theory that the same gene or genes are influencing fat production in both studies. In a similar way, studies by Casas et al. (2000), Ashwell et al. (2001), Rodriguez-Zas et al. (2002), and Moore et al. (2003) detected a QTL for fat production on chromosome 14. Casas et al. (2000) identified a QTL for fat thickness between centimorgans 10 and 20 on chromosome 14. Ashwell et al. (2001) reported an association of marker BMS1678 with daughter deviation fat, and daughter deviation percentage fat. This marker is located at 6.2 centimorgans from the beginning of the linkage group on chromosome 14. In addition, Rodriguez-Zas et al. (2002) detected QTL for fat yield daughter yield deviation in two families on centimorgans 0 and 17 of the same chromosome. Moore et al. (2003) detected a quantitative trait locus for backfat in the centromeric region of bovine chromosome 14. However, the support interval for the fat thickness QTL detected on this chromosome in the present study indicates that its most likely position is between centimorgans 0 and 16. Quantitative trait loci from previous studies are included within the support interval. It is feasible that this region harbors genes responsible for fat production, regardless of specialization (beef or dairy) in cattle.

Two candidate genes reside at the centromeric region of chromosome 14 for fat production. The first is the DGAT1 gene, which has been associated with an effect on milk fat content in dairy cattle, (Grisart et al., 2001). The second is the TG gene (Barendse, 1999). McPeake (2003) indicates that this gene has been associated with intramuscular fat deposition in long-fed cattle. However, Moore et al. (2003) found both genes to be independently segregating from fat thickness in three independent populations. These conflicting results may indicate that the mutations at these genes may not be the cause of differences in the expression of fat production. Other mutations within these or other genes should be responsible for the effect in fat production.

Retail product yield is an estimate of amount of saleable product from a given carcass and is considered an important carcass composition trait. Evidence of a significant QTL and evidence suggesting presence of four additional QTL for this trait were detected in this study. Stone et al. (1999) using a proportion of offspring from this family, selected for extremes of the phenotypic distribution for retail product yield, had identified the QTL on chromosomes 13 and 18. However, Stone et al. (1999) did not detect QTL on chromosomes 9, 19, and 29. This highlights the importance of using all members of a family or population in the detection of QTL, although selective genotyping is still useful for scanning the genome in an efficient, expedient way (Bovenhuis and Spelman, 2000).

Two significant QTL were detected for longissimus area, one on chromosome 5 and the other on chromosome 6. There are no previous reports of QTL for this trait on these chromosomes. The one on chromosome 5 lies within the region where QTL have been detected for birth weight, marbling, and fat yield in the present study. Casas et al. (2000) had previously identified QTL for fat thickness, USDA yield grade, retail product yield, and meat tenderness in offspring from a Piedmontese × Angus sire. Although QTL from both studies lie in the same genomic region, it would be expected that different genes are affecting different traits. Significant QTL for longissimus area are important because this trait is of great value in the beef industry. Further studies need to be pursued to identify genes responsible for these QTL.

Five chromosomes harbor QTL associated with birth weight. The loci on chromosomes 5 and 21 were significant, and there was evidence suggesting the presence of others on chromosomes 1, 2, and 3. Davis et al. (1998) reported significant QTL for birth weight on chromosome 21. Davis et al. (1998) used three half-sib families from Charolais × Brahman bulls. Their most significant QTL was at 4 centimorgans from the beginning of the linkage group on chromosome 21. This is the same position in which the most significant QTL for birth weight in this study was detected. The effect of this QTL on the study by Davis et al. (1998) was 3.3 kg in one family. This effect is similar to the one found in this study. It is likely that the same gene or group of genes is responsible for the effect on birth weight in both studies. Kim et al. (2003), using a random model in a Brahman and Angus crossbred population, found a QTL for birth weight on chromosome 21; however, the location was at 62 centimorgans from the beginning of the linkage group, which is telomeric when compared with the one found in the present study. This indicates the presence of a QTL for birth weight on chromosome 21.

Evidence indicates the presence of a QTL for birth weight on chromosome 5. Kim et al. (2003) detected a QTL for birth weight at centimorgan 49 from the beginning of the linkage group of this chromosome. The interval bracketed by the markers used by Kim et al. (2003) roughly correspond to the support interval estimated in the present study. This indicates that the same QTL has been identified in two independent populations. The additive effect of the QTL indicates that offspring inheriting the Brahman allele are heavier at birth than offspring inheriting the Angus allele. In the present study, the offspring inheriting the Brahman allele were heavier than the offspring inheriting the Hereford allele. Li et al. (2002) associated marker haplotypes on chromosome 5 with birth weight. One haplotype was located between centimorgans 65 and 74. The markers used in the study by Li et al. (2002) also correspond to the support interval from the present study. Davis et al. (1998) reported the existence of a QTL on this chromosome, but their location seems telomeric when compared with the one in the present study. The maximum LOD score in the paper by Davis et al. (1998) is at 90 centimorgans from the beginning of the linkage group. The support interval for the QTL for birth weight in the present study does not include this position. Machado et al. (2003), using a composite breed developed from the cross of *Bos indicus* and *Bos taurus*, detected a QTL for birth weight between markers ILSTS066 and BMS1248. This location corresponds to the interval between centimorgan 72 and 84 of the linkage group. The position of the QTL detected by Machado et al. (2003) lies between the one detected in the present study and the one by Davis et al. (1998). It is possible that more than one QTL for birth weight is segregating in this chromosome.

Detection of QTL for birth weight on chromosomes 5 and 21 was done mostly in crossbred families between *Bos taurus* and *Bos indicus*. No QTL for birth weight were identified by Grosz and MacNeil (2001), Casas et al. (2000), and Casas et al. (2001) using crossbred populations from *Bos taurus*. However, QTL for birth weight have been detected when scans involved crossbred animals, between *Bos taurus* and *Bos indicus*, with the exception of the study by Li et al. (2002), as is the case with the report by Davis et al. (1998), Kim et al. (2003), Machado et al. (2003), and the present study. It is probable that the frequency of the alleles at the gene or genes that could cause this difference among *Bos taurus* crosses are in low frequency, thus rarely detected. The QTL can be easily detected when crosses between *Bos taurus* and *Bos indicus* are involved.

Stone et al. (1999) had previously detected suggestive QTL for birth weight on chromosome 1 when a preliminary scan for growth and carcass traits was done in this family. They indicate that those individuals inheriting the Brahman allele were heavier at birth. Given that Stone et al. (1999) used a selected proportion of the animals to be genotyped, they did not report magnitude of the effect. We now know that individuals inheriting the Brahman allele are 2.6 kg heavier at birth.

A QTL for birth weight was detected on chromosome 2. Grosz and MacNeil (2001) detected a QTL for the same trait on this chromosome. The QTL from the present study seems to be centromeric when compared with the one from the study by Grosz and MacNeil (2001). They indicate that the most likely position of the QTL is between centimorgans 106 and 120 from the beginning of the linkage map. This position is excluded from the support interval from this study. It is possible that two QTL for birth weight may be segregating on chromosome 2.

Implications

Quantitative trait loci for growth and carcass traits have been detected on several chromosomes. Several are located in chromosomal regions where previous studies have indicated the presence of quantitative trait loci. Regions reported here to contain quantitative trait loci need to be assessed in outbred populations to determine the extent of their usefulness in selection programs in which genetic marker information is to be used.

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